The Report Committee for Stephen Edward Goodyear Jr.
Certifies that this is the approved version of the following report:

Variation in diet and habitat resource use in desert adapted lizards in Western Australia

APPROVED BY
SUPERVISING COMMITTEE:

Supervisor:

Eric R. Pianka

Norma L. Fowler

Variation in diet and habitat resource use in desert adapted lizards in Western Australia

by

Stephen Edward Goodyear Jr., B.S. Zoo.

Report

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

Master of Arts

The University of Texas at Austin

August 2011

Dedication

I dedicate this work to the lizards that sacrificed everything so that I could learn about how they lived.

Acknowledgements

Firstly, I thank Esperanza Florendo for living with me while I completed this work. Second, I thank Gisela Kaufmann and Carsten Orlt of Kaufmann Productions for contributing a large portion of funding that allowed me to conduct fieldwork in Australia.

For assistance in preparing this report I thank my committee members, Eric Pianka and Norma Fowler. I also thank Chris Bell, Jeremy Brown, and Alison Gainsbury for reviewing early versions of this work. All data related to this report come from lizards collected in the Great Victoria Desert in Western Australia by Eric R. Pianka over a three decade-long period.

For providing assistance in fieldwork I thank Laurie Smith, Graham Thompson, Karl Brennan, Brad Maryan, Stephen Argus and his family, Harvey Sunter-Smith, Christian Rutz, Lucas Bluff, Malcolm Ludgate, Hugh Bland, Anke Frank, Chris Bell, Jim Mead, Ruth Allen and Clive, Beckie Symula, Tangerine, and Matilda.

For providing assistance on my microfossil work unrelated to my Master's report I thank Bridget Wade, Paul Pearson, Andy Purvis, David Lazarus, Jack Baldauf, Li-Hsiang Liow, John Alroy, and the 2006 instructors and students of the summer program in paleontology and statistics at the National Center for Ecological Analysis and Synthesis.

I thank those people who contributed a great deal to my education in biology and research; including Harold Heatwole, Marianne Niedzlek-Feaver, Margret Leftwridge, Jeremy Feinberg, and the 2004 cohort of interns in the environmental biology group at Brookhaven National Laboratory.

Lastly, I offer compassionate thanks to every graduate student in the programs of Ecology, Evolution, and Behavior and Plant Biology at The University of Texas at Austin, including all past students who I have met and future students of these programs who I may meet in the future.

Variation in diet and habitat resource use in desert adapted lizards in Western Australia

Stephen Edward Goodyear Jr., M.A.

The University of Texas at Austin, 2011

Supervisor: Eric R. Pianka

Abstract: Impacts of ecological competition are reduced when organisms play different roles in their environment. More individuals can survive on varied but finite sets of resources when organisms eat different kinds of prey, live in different places, or are active at different times. Species within an assemblage of small fossorial snakes have ecologies that vary mostly by diet. Different species eat very different things. Species live in different habitats on sand ridges, but the differences are less dramatic than in diet. Disparity in resource use typically varies the most according to species, so that individuals of the same species are more similar to each other than they are to individuals of other species. However, variation exists in resource use within species over time and space. Wide variation exists in dietary resource use in four well-sampled species of comb-eared skinks. However, where species occur at the same study site there are clear distinctions in resource use between species despite the wide variation in diets observed between individuals of the same species. Additionally, strict ecological distances in diet between species are maintained during five censuses that were conducted over a 16-year period. These results illustrate the basic ecological principals of fundamental and realized niches. Here, individuals ate many different food items and species have the potential to

overlap in diet but that overlap is reduced because of realized ecological boundaries between species within a single place and time, which result in decreased competition for resources.

Table of Contents

List of Tables

List of Figures

Chapter 1: *Sympatric Ecology of Five Species of Fossorial Snakes in Western Australia*

INTRODUCTION

Squamates are useful model organisms in studying sympatric ecology (Fitch, 1975; Huey et al., 1983; Pianka, 1969, 1971, 1973, 1974, 1975; Shine, 1977). Most of these studies of sympatry include only non-ophidian squamates ("lizards"). Much remains unknown about how snakes partition resources within species-dense communities. Squamates are useful models in comparative ecological studies because: (1) most species are relatively abundant, (2) they are easily trapped, and (3) most species eat prey whole, making identification of stomach contents manageable. Data on sympatric ecology of snakes, in relation to non-ophidian squamates, are generally lacking because snakes are less abundant, more cryptic and often have empty stomachs. However, resource partitioning in the form of habitat, food, and time has been documented in several snake assemblages (Carpenter, 1952; Fouquette, 1954; Henderson, 1974; Luiselli, 2006 and references therein; White and Kolb, 1974). Snakes have different behavioral and ecological attributes compared to other lizards and greater knowledge of sympatry in snakes could be useful in understanding complexities of community structure.

We present spatial, reproductive, and dietary data for five sympatric fossorial elapids of the *Simoselaps – Brachyurophis – Neelaps* clade from the Great Victoria Desert in Western Australia. Data on ecologies of these five snakes are limited and nothing is known about their behavior in sympatry. Previous studies (Scanlon and Shine,

1988; Shine, 1984; Strahan et al., 1998) have used museum specimens where individuals had been collected throughout their ranges, including many areas where the five species included in our study are not sympatric. Shine (1984) showed that *Brachyurophis semifasciatus* specialize on squamate eggs while the other four species consume long, slender adult lizards, especially *Lerista* sp. (Scincidae) and various *Ctenotus* skink species. How and Shine (1999) conducted censuses of five *Simoselaps* species at 32 sites near Perth, Western Australia over 11 years. Four species in their sample overlap with species in our assemblage, but not all species were found at every site. How and Shine (1999) emphasize differences among species and sexes in seasonal time of activity and species composition at different sites. Data on species differences in dietary or microhabitat preference in sympatry are not presented by How and Shine (1999), which are the emphases of our study. Here, we will test whether data on diets from these five snakes in sympatry agree with data presented by Shine (1984) where these five snakes were not necessarily sympatric. In addition, we present data on differential use of microhabitats on sand ridges, which were not provided by Shine (1984) and Scanlon and Shine (1988), and some data on reproductive ecology.

Resource dimensions are traditionally categorized as habitat, food, and time of activity (Pianka, 1973, 1975). In a comprehensive literature review of resource partitioning studies on amphibians and reptiles, Toft (1985) determined habitat as the most partitioned resource dimension in most taxa except amphibian larvae and snakes. Diet, in snakes, is the most important dimension in reducing ecological overlap among species. These data agree with previous reviews (Arnold, 1972; Schoener, 1977) that diet/predation is most important for ecological divergence in snake assemblages. Luiselli (2006) reviewed literature published on resource partitioning in snakes since Toft's review and concluded that diet is the most partitioned resource in 56.8% of studies. We

will combine data on different resource dimensions to test if diet is the most important resource dimension in this fossorial snake assemblage. Resource partitioning may not be a consequence of competition alone, but may be influenced by variation in physiological and morphological constraints, response to predators (Toft, 1985), and historical constraints (Brooks and McLennan, 1991)

METHODS

Specimens were collected in the field by ERP using pit fall traps and by hand during ten Austral spring and summer seasons over 25 years between 1978 and 2003 (i.e., 1978-1979, 1989-1992, 1995-1996, 1998, 2003). Table 1 outlines number of trapdays, census durations for individual collecting periods, and species census data. Not every trap is open during the entire census. The study site is a large, semi-pristine red sand desert in the Great Victoria Desert of south-western Australia (28°12'S, 123°15'E). Topography is punctuated by large sand ridges with shallow rises and steep slopes, with interdunal flats covered mostly by spinifex grass with scattered marble gum trees. Vegetation on sandridges consists primarily of various shrubs (refer to Pianka [1986: 9-11] for further description of the study site). Series of pit fall traps cover all habitats and areas of the ridges and flats at the study site. Designated microhabitats on sandridges and number of pit traps at each location (*N*=) are crest (33 [top of ridge]), slope (9), base (24), and flat (11 [area between dunes]). Pit traps were checked 2-3 times daily. Snakes reported herein were found during early AM checks and are thus nocturnal. An associated pit fall trap number was recorded for every snake collected, providing data on microhabitat and position on sand ridges. Snakes were preserved and later dissected and analyzed for stomach contents, testes sizes in males, and numbers and volumes of eggs in females. All

dissected parts, including stomach contents and eggs, were counted and measured by volume (nearest tenth of a cubic centimeter) and length (nearest tenth of a millimeter) and placed in separate containers from the whole snakes. Relative clutch mass (RCM) was calculated by dividing total egg volume by total adult body mass.

Relative importance of resource dimensions was determined by comparing niche overlaps, as calculated by Pianka (1973, 1974), among species. Dimensions having less overlap identify those dimensions that may be key to phenotypic divergence among species and hence, ecological diversification.

RESULTS

Data on habitat use reveal that some species specialize on certain habitats while others are more microhabitat generalists (see Fig. 1). *Simoselaps anomalus* were trapped 63% of the time on the crest area of sand ridges and less frequently on the three other areas of the ridges. *Simoselaps bertholdi* and *Brachyurophis semifasciatus* were trapped an almost equal amount in each microhabitat. *Brachyurophis fasciolatus* and *Neelaps bimaculatus* were trapped nearly half the time on slopes, but never on flat areas.

S. anomalus and *S. bertholdi* consume almost exclusively (over 90%) *Lerista* sp. lizards. All fully intact *Lerista* in stomach contents were identified as *Lerista bipes*, which is distinguishable from other local *Lerista* species by the presence of two digits on its hind limbs. Many *Lerista* found in stomachs were partially digested or only contained autotomized tails, so were unidentifiable to species level. All *Lerista* found in stomach contents were oriented head-first. The only stomach content identified in any specimen of *N. bimaculatus* was the tail of a *Ramphotyphlops* snake. *B. semifasciatus* ate almost exclusively squamate eggs, with the exception of one unidentifiable hard, amber-colored

object. Eggs were identified as belonging to squamates because of the soft, leathery cover characteristic of most squamate eggs, and several eggs were discovered that still had embryos, recognizable as lizards, inside them (see Table 2 for diet summaries).

Reproductive data, including testes sizes, egg numbers and egg volumes were measured in all five snake species (Table 3). In males of each species, testes size correlated positively with SVL and fresh body mass ($P < 0.002$). For gravid females of each species, neither egg number nor total egg volume correlated with SVL or mass ($P > 0.1$) except for *B. semifasciatus* where fresh body weight correlated positively with total egg volume ($R^2 = 0.65$, $P < 0.001$). Mean clutch size (number of oviductal eggs) varied little among species (3 – 4.67). However, relative clutch mass (volume of eggs in proportion to total adult weight) varied more widely (3 – 13%) among species. Sex ratios in samples of all species were male biased (ranging from 61-86% among species) and percentages of females collected that bore oviductal eggs ranged widely from 17 to 100% among species (Table 4).

Comparisons of resource dimensions reveal diet as a greater structuring agent than habitat use. Treating individual species as cases, habitat niche overlap is significantly greater than dietary niche overlap (Wilcoxon signed-rank test, $W = 10$, $P < 0.005$; see Table 5 for all species pairwise comparisons). As a temporal dimension, seasonal activity does not vary substantially among species. Individuals of all species were collected most often in December except for *B. fasciolatus*, most of which were collected in November. While all species are nocturnal, precise information is not available for exact activity time on a daily cycle.

DISCUSSION

Several features stand out in our diet and microhabitat data. First, *Lerista* make up 66% of prey by number (69% by volume) consumed by all snakes, with most being *Lerista bipes*. These data confirm data presented by Shine (1984) that *Lerista* compose a substantial dietary component in these species. *Lerista* and all five snake species in this study are fossorial, spending most of their time burrowing under or "swimming" through sand, which should result in a great chance of habitat overlap and for these animals to encounter one another. However, some snake species in this study are more fossorial than others, which may contribute to variation in overlap of resource use. *Neelaps bimaculatus* is more of a "swimmer" than a burrower (E. R. Pianka pers. observ.) and the other species vary in size of the rostral shield and morphology of countersunk jaw kinesis (Scanlon and Shine, 1988), which may indicate degree of fossoriality. Secondly, our data confirm Shine (1984), that *B. semifasciatus* is a dietary specialist on squamate eggs.

In this assemblage, *B. semifasciatus* is the only complete dietary specialist, but is a habitat generalist. Lack of dietary competition may enable *B. semifasciatus* to exploit food resources in all microhabitats whereas other species specialize on sandridge crests. Alternatively, distributions of snake species may simply reflect either distributions of most commonly used dietary resources or loose substrate on sandridge crests more suitable for burrowing. From this same locality, Pianka (1996) reported *L. bipes* were caught most often in traps on sandridge crests (42.5%), less often on sandridge bases (38.8%), and much less often on slopes and flats (15 and 3.7%, respectively; $N = 614$). These data conform to the hypothesis that microhabitat use of elapid snakes tracks that of their prey. Lastly, the only invertebrate consumed by any snake was one ant by *S. bertholdi*, which was likely consumed inadvertently along with a *Lerista*. *Ctenotus* skinks were also found to be a minor part of diets of the two *Simoselaps* species, differing from

data given by Shine (1984) which show that *Ctenotus* make up a major prey source for all five snakes except *B. semifasciatus* (the egg specialist). It is not clear why snakes in this study consumed fewer *Ctenotus* skinks. Since these snakes are nocturnal and *Ctenotus* skinks are diurnal it is peculiar that they were found so frequently in diets of snakes analyzed by Shine (1984). Temporal partitioning between these snakes and *Ctenotus* skinks may reduce interaction and, hence predation of small skinks. However, at this study site thirteen *Ctenotus* skink species occur including five that could be considered abundant. Given their abundance we might expect more snake predation on *Ctenotus* skinks than observed in this study.

No single ecological parameter shapes an entire assemblage. Abundance and diversity for any group of organisms are likely influenced by more factors than analyzed here. However, a quantitative attempt can be made to answer which ecological dimensions are most important in shaping apparent ecological diversity within communities. Pairwise comparisons between species of habitat niche overlap and dietary niche overlap allow inference of which factors have greater effect on community structure (Pianka, 1973, 1974). Here, diet is a much greater structuring agent than is habitat use. These results match the consensus that most snake assemblages are structured by diet (Luiselli, 2006; Toft, 1985). However, some authors have questioned whether interspecific competition plays any significant role in structuring communities (see Reichenbach and Dalrymple, 1980 for a concise argument).

Our study suffers from several shortcomings. Most notably, we had low sample sizes for some species. *B. fasciolatus* and *N. bimaculatus* are represented by only 22 and 14 specimens, respectively. Only two specimens of *B. fasciolatus* and one specimen of *N. bimaculatus* contained any stomach contents. Limited dietary data give a likely incorrect representation of resource use and dietary specialization in these two species. Another

limiting factor in our study is that specimens were collected mostly during the Austral spring seasons, when abundance and activity are high and many animals were likely to be caught in pit fall traps. However, during Austral winter collections in 1992, none of these snake species were ever found in a pit trap. Lastly, although pit fall traps have been shown to be useful in catching squamates, especially cryptic species, they have many drawbacks (Enge, 2001). A major disadvantage of using pit fall traps is that one cannot elucidate the exact moment that an animal was trapped and, therefore, one cannot know the animal's precise time of activity. One can only assume that an animal has been caught in a trap sometime since the trap was last checked. Along with this, data on temperature, humidity, etc. are useless in understanding any correlation between such environmental factors and animal activity. Another drawback to pitfall traps is that some animals may die in traps as a result of environmental factors and predation and not preserve well. Lastly, some individuals might be resistant to pit fall trapping methods. Further, one cannot undergo a thorough comparative ecological study without taking into account phylogeny (Felsenstein, 1985). Previous attempts have been made to reconstruct phylogenies of Australian elapids by using morphological (Keogh, 1999) and molecular data (Keogh et al., 1998), but do not include more than two species from the entire *Simoselaps – Brachyurophis – Neelaps* clade. A more detailed phylogeny of this group will be required to sort out effects of ecology and historical inertia in determining behaviors and habits of these snakes.

Year	Trap Days	Census period	Species										Total
			S. anomalus		*S. bertholdi*		*B. fasciolatus*		*B. semifasciatus*		*N. bimaculatus*		
			N	*N/100p*	*N*	*N/100p*	*N*	*N/100p*	*N*	*N/100p*	*N*	*N/100p*	
1978-79	none	30 Jul - 13 Mar	0	-	2	-	1	-	3	-	0	-	6
1989-91*	8646	8 Oct - 6 Mar	47	0.54	13	0.15	0	0.00	12	0.14	1	0.01	73
1992	3885	30 Jul - 15 Dec	25	0.64	13	0.33	5	0.13	0	0.00	0	0.00	43
1995-96	5714	12 Sep - 8 Feb	31	0.54	10	0.18	2	0.04	17	0.30	2	0.04	62
1998	7600	14 Sep - 5 Dec	34	0.45	20	0.26	8	0.11	14	0.18	6	0.08	82
2003	3849	9 Sep - 5 Dec	0	0.00	4	0.10	6	0.16	5	0.13	5	0.13	20
			137		62		22		51		14		286

Table 1: Species census and relative capture rates.

Species census and relative capture rates per 100 pitdays [= (N/100p)] through six census periods.

* lapse in trapping between 24 February 1990 - 5 September 1990

Sp. / Diet		*S. anomolus*	*S. bertholdi*	*B. fasciolatus*	*B. semifasciatus*	*N. bimaculatus*	Totals
Lerista sp.	N	29 (96.7%)	14 (82.4%)	0	0	0	43 (66.2%)
	V	7.95 (98.8%)	5.25 (90.5%)	0	0	0	13.2 (68.8%)
Ctenotus sp.	N	1 (3.3%)	1 (5.9%)	2 (100%)	0	0	4 (6.2%)
	V	0.1 (1.2%)	0.45 (7.8%)	0.35 (100%)	0	0	0.9 (4.7%)
Ramphotyphlops sp.	N	0	0	0	0	1 (100%)	1 (1.5%)
	V	0	0	0	0	0.1 (100%)	0.1 (0.5%)
Eggs	N	0	0	0	14 (93.3%)	0	14 (21.5%)
	V	0	0	0	4.7 (95.9%)	0	4.7 (24.5%)
Invertebrates	N	0	1 (5.9%)	0	0	0	1 (1.5%)
	V	0	0.1 (1.7%)	0	0	0	0.1 (0.5%)
Unidentified	N	0	1 (5.9%)	0	1 (6.7%)	0	2 (3.1%)
	V	0	*	0	0.2 (4.1%)	0	0.2 (1.0%)
Empty stomachs		114 (83.2%)	47 (75.8%)	20 (90.9%)	36 (70.6%)	13 (92.9%)	230 (80.4%)
Totals	N	137	62	22	51	14	286
	V	8.05	5.8	0.35	4.9	0.1	19.2

Table 2: Numbers and volumes of prey types.

Numbers (N) and volumes (V) of prey type (percentage of total amount consumed in parentheses) in the diet of each snake species. Also shows number and percentage of snakes found to have empty stomachs.

* indicates a negligible amount of food content in stomach

Species	*N*=	SVL (mm)	CS	RCM
S. anomalus	13	190.69 ±2.06	3 ±0.2	9% ±1.86
S. bertholdi	6	255.67 ±6.3	4.67 ±0.49	13% ±4.06
B. fasciolatus	1	285.00	3	6%
B. semifasciatus	15	304.8 ±7.59	3 ±0.24	3% ±0.8
N. bimaculatus	2	405.00	4	9%

Table 3: Means and standard errors for body and egg size in females.

Means and standard errors for SVL, clutch size (CS), and relative clutch mass (RCM) in proportion to weight for fecund/gravid females. Standard errors are not given for *B. fasciolatus* and *N. bimaculatus* due to our small sample sizes for these species.

Species	*N*=	% male in Pop.	% female in Pop.	% of Fecund female
S. anomalus	137	0.80	0.15	0.65
S. bertholdi	62	0.61	0.39	0.17
B. fasciolatus	22	0.86	0.09	0.50
B. semifasciatus	51	0.65	0.35	0.83
N. bimaculatus	14	0.79	0.14	1.00
Total / Average	286	0.73	0.23	0.55

Table 4: Sex ratios as percentages of the population.

Sex ratios as percentages of the population for each species including percentage of females that bore oviductal eggs. Percentages for some species do not add up to 100% because sex could not be determined for some small juveniles.

Species	*S. anomalus*	*S. bertholdi*	*B. fasciolatus*	*B. semifasciatus*	*N. bimaculatus*
S. anomalus	-	0.884	0.836	0.658	0.893
S. bertholdi	0.997	-	0.875	0.885	0.885
B. fasciolatus	0.034	0.071	-	0.900	0.989
B. semifasciatus	0.000	0.000	0.000	-	0.843
N. bimaculatus	0.000	0.000	0.000	0.000	-

Table 5: Pairwise comparisons of habitat and diet use.

Pairwise comparisons between each species indicating amount of habitat niche overlap (captures per trap in each microhabitat) on the top right of the diagonal and dietary niche overlap (based on number of prey items in diet) on the bottom left of the diagonal.

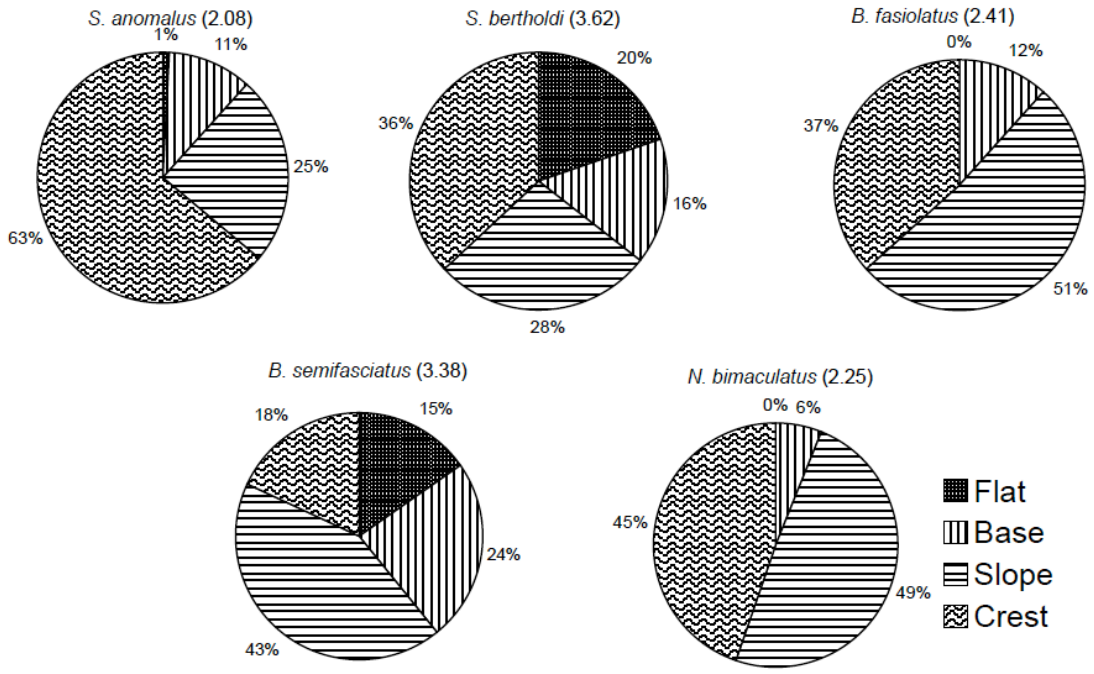

Figure 1: Proportional habitat use.

Different regions of pie chart represent percentage of samples collected at one of four microhabitats as indicated in the legend (numbers in parentheses indicate niche breadths as calculated by the reciprocal of Simpson's diversity index, H' $(1 / (\Sigma p^2))$. Capture rates are determined as proportions relative to number of pit traps in each microhabitat. Numbers of traps (N =) at each microhabitat are: Flat (11), Base (24), Slope (9), Crest (33).

Chapter 2: *Spatial and temporal variation in diets of sympatric lizards in Western Australia*

INTRODUCTION

Variation in species use of dietary resources, both geographically and through time, adds to the complexities of community structure and species interactions. Consider even the most detailed food web that shows links between consumers and resources with proportions of interactions between links. Diet variation implies that moving that same food web model to a different location or tracking it through time results in, at least, changing the proportions of interactions between links and possibly deleting or adding links between species. A greater understanding of degree of diet variation observed in natural populations will enhance knowledge of the lability of food webs. Changes in food web dynamics are crucial to any consideration of stability and complexity as emergent properties of communities.

Variation of any population attribute can be studied within and among populations at different locations or over time. Studies of amphibians and reptiles have contributed a large proportion of what is known about diet variation. In a review of published studies on resource partitioning in amphibians, squamates, and turtles, Toft (1985) found food to be a partitioned resource in 36% (N = 16) of lizard studies and important to some degree in 94% (N = 45) of studies. Only snakes partition food resources more finely than lizards. Habitat is the most partitioned resource in 53% (N = 24) of lizard studies. Here, we examine variation in use of dietary resources and consider

how changes in diet impact generalities inferred about species resource use from isolated samples. Diet in amphibians, squamates, and fishes is relatively easier to obtain and more reliable than dietary data from other vertebrates. Ectotherms consume prey whole, or mostly whole, and lower energy requirements mean consumed prey items remain stored in stomachs for a longer time as compared to endotherms. We restrict our review of past diet studies to turtles, squamates, and amphibians, but cite notable studies on other vertebrate groups.

In a spatial context, diet variation has been studied in lizards (How et al., 1986; Klawinski et al., 1994; Mesquita and Colli, 2003; Vitt and Colli, 1994; Vitt et al., 1998), snakes (Beaupre, 1995; Bowen, 2004; de Queiroz et al., 2001; Fillipi et al., 2005; Luiselli et al., 2007; Tuttle and Gregory, 2009; Weatherhead et al., 2009), a salamander (Zerba and Collins, 1992), and frogs (Bonansea and Vaira, 2007; Leavitt and Fitzgerald, 2009; Mahan and Johnson, 2007; Siqueira et al., 2006). Studies of diet change through time have been conducted for lizards (Christian et al., 1984; Hibbitts et al., 2005; James, 1991, Pianka and Goodyear, *in press*), snakes (Garcia and Drummond, 1988; Kephart and Arnold, 1982), a frog (Valderrama-Vernaza et al., 2009); and the loggerhead sea turtle, *Caretta caretta* (Seney and Musick, 2007). In some studies, diet variation over space and time was recorded concurrently in lizards (Parker and Pianka, 1975; Pianka, 1970; Rodríguez et al., 2008; Vitt et al., 1981) and angulate tortoises (Joshua et al., 2010).

Most studies consider either spatial or temporal dimensions in a single analysis. Population variation observed over two or more dimensions will add extensively to total variation observed between samples. The herpetological literature is lacking in such multi-dimensional analyses of diet variation. However, studies on fish in Venezuela (Winemiller 1990) and France (Ferraton et al. 2007) are the most integrative investigations of diet variation over multiple dimensions and may set the groundwork for

future herpetological studies on this subject. Winemiller (1990) demonstrated dynamic connectance in freshwater fish food webs in Venezuela by studying fish diets during three intra-annual seasons. Winemiller (1990) found that food webs varied in content and connectance between dry and wet seasons as well as among study sites. Ferraton et al. (2007) found great dietary shifts over a year at seven sampling locations in the fish, *Merluccius merluccius*, in the Gulf of Lions of southern France. Ferraton et al. conclude that factors contributing most to diet variation are depth, year, and location along the shore (in decreasing order of importance). Fish forage over a more 3-dimensional space compared to terrestrial amphibians, squamates, and mammals, so unsurprisingly, differences in water depth exhibit the strongest variation in diet between samples. Using stable isotopes, Ferraton et al. (2007) conclude that diet change over one year contributed more variation in their system than spatial variation between four collecting zones (farthest separated by about 200 km). Ability to rank importance of dimensions that contribute to diet variation is necessary for community stability studies as well as management efforts to conserve maximum biodiversity. Unfortunately, such all-inclusive studies are rare and most, as identified in the herpetological literature, focus on a single dimension at a time.

We present data on variation of diet in four congeneric Australian desert scincid lizards over space between three collecting locations and through time from five censuses over a 16-year span. We chose these species because of their relatively large sample sizes at each location. Additionally, we chose to restrict our study to species within the genus *Ctenotus* to reduce phylogenetic dependencies of data when comparing species.

METHODS

Lizards were collected at three separate sites within the Great Victoria Desert of Western Australia, all within 100 km of one another. Sites were chosen based on each having specific habitat differences to evaluate roles of vegetation cover and sand ridges on lizard species diversity. The R area ("Redsands") is named for its red sand ridges. Vegetation is mostly spinifex grass (*Triodia basedowi*) with few *Eremophila, Grevillea* and *Thryptomene* bushes and Marble Gum (*Eucalyptus gongylocarpa*) and Mulga (*Acacia aneura*) trees interspersed. Approximately 4 km South of the R area is the B area, named for being the site of a large experimental burn. No sand ridges or trees occur at the B area. The B area was chosen to represent a homogenous landscape to compare to the heterogeneous topography and vegetation found at the R area. It was first sampled in 1992 when it had long unburned mature old spinifex, and then it was burned experimentally in 1995. The L area (40 km East of Laverton) is about 100 km West of the B and R areas. The L area is a flat sandplain with many of the same habitat features as Redsands except it lacks sandridges. Further descriptions of two sites, the L and R areas, can be found in Pianka (1986, chapter 1).

All *Ctenotus* skinks were captured using pit traps. Linear series of traps spaced approximately 10 m apart were laid with associated drift fences. Number of traps varied at the three sites as follows: B-area (N=75), L-area (75 initially, later increased to 100), and R-area (77, later increased to 100). Traps were checked twice daily nearly every day for 70-100 days each over five Austral Spring seasons. Censuses were conducted between August and no later than February in 1992, 1995-1996, 1998, 2003, and 2008. Traps were closed during any layover in collecting. All squamates caught in traps were sacrificed, preserved, catalogued by the Western Australian Museum and later shipped to The University of Texas at Austin for laboratory analyses. All collecting was done with

the approval of appropriate animal welfare authorities under permits issued by the Department of Conservation and Land Management (CALM).

Most or all individuals of the 4 *Ctenotus* species from different areas and times were dissected and stomach contents were analyzed. Items within stomachs were sorted among 23 categories; including common orders of arthropods, vegetation, vertebrates, unidentified objects, and inadvertently consumed pieces of wood and rocks. Items were counted and volumes estimated to the nearest cubic millimeter for each category. Volumes were estimated by placing a one millimeter thick layer of material over square millimeter grid paper and approximating total volume. Each lizard's counted stomach contents were kept individually and stored in ethanol. Dietary niche breadths were estimated using Simpson's index of diversity [$D = 1/ \Sigma p_i^2$] where p_i is the proportion by volume of food items in stomachs based on 23 prey categories.

Principal Components Analyses (PCA) were performed to extract the most important components of dietary niche space. For each species, a table with seven rows (each sample of lizards) and 23 columns (each diet category with volumetric stomach contents computed as relative proportions) were input and computed to return PCA scores and Euclidean distances between samples for construction of dendrograms. Each PCA returned seven component scores, one for each row or item examined. Scores on the first two principal components representing the greatest proportion of variance are shown graphically.

RESULTS

Stomach contents were sorted into 23 discrete categories. Items in some categories were not consumed or consumed very irregularly by certain species. Figure 1

displays percent abundances of the seven overall most common dietary resources used by each of these four species. Three key aspects of diet variation stand out in these graphs. First, variation is great across species. The most common resources consumed by one species may be hardly utilized by another. For example, *Ctenotus calurus* and *Ctenotus pantherinus* consume more Isoptera (termites) compared to *Ctenotus piankai* which eats Hemiptera (bugs) and *Ctenotus quattuordecimlineatus* consume more Orthoptera and Aranae (spiders). Second, diets of all species vary across sites. Shaded bars in the left column of Figure 1 show diets from the three study sites. For *C. calurus* and *C. piankai,* diet is relatively consistent across sites compared to diets of the other two species. Third, diets vary through time. Figures in the right column show diets for lizards captured on the B-area during each of the five censuses. Diet in every species varies between sampling intervals.

Relative contributions to diet variation by space and time dimensions are depicted in Figure 2. Results from a principal component analysis and a cluster dendrogram based on Euclidean distances are shown for each species. Cluster analyses include data from all 23 diet categories. In only one case, *C. piankai*, data from across sites from the same year cluster together entirely (inside solid square on dendrogram). A cluster of all 1992 samples is nearly met for *C. calurus* and *C. quattuordecimlineatus*, but samples from the other times break up the 1992 across sites cluster (squares with dashed lines).

Another way of depicting diets is shown in Figure 3, where samples of all species were combined in a single PCA to show positions of species in dietary niche space through both time and space (Fig. 3). The first two components reduce variation by 60% (PC3 contributes a further 13%, not shown). Positions of each of the five prey categories that most reduce variation in diet are shown in bold type. PC1 loads primarily on a Hemiptera-Isoptera axis whereas PC2 loads on a Hemiptera-Orthoptera-Aranae axis. *C.*

piankai and *C. quattuordecimlineatus* cluster on the left and *C. calurus* on the right. *C. pantherinus* is intermediate. Samples for each species cluster together within relatively small areas of total niche space, demonstrating dietary consistency. Two pairs of species exhibit some overlap: *C. piankai* and *C. quattuordecimlineatus* overlap more with each other than they overlap with the other two species, as do *C. calurus* and *C. pantherinus*.

DISCUSSION

Analysis of food web structure and species connectivity within a community is incomplete without considering variation in species interactions. Estimated realized dietary niche of each of these lizard species varies over space and time. Variation in how species interact may be important in determining how food webs bend and flex without breaking down completely and how communities show resiliency in the face of major environmental changes. Realized dietary niche may change at any particular site or year, as represented by individual points in figure 3, but each species consumes prey resources within the bounds of its own fundamental niche space. *C. calurus* and *C. pantherinus* subsist mainly on termites and larvae, *C. pianka* eats mosty true bugs, and *C. quattuordecimlineatus* consumes more conspicuous items such as spiders and grasshoppers. The limited amount of overlap between species in dietary niche space implies fundamental ecological differences between species that may not be overturned by short-term environmental variation. Each species appears to be tied to one or two food types that comprise the bulk of their diets.

Wildfires in the arid Australian interior are large and cause major changes in vegetation composition (Haydon et al., 2000; Whelan, 1995). Several authors have recorded subsequent changes in lizard species compositions following fires in arid (Fyfe,

1980; Masters, 1996) and tropical (Braithwaite, 1987) regions of Australia. The relative importance of diet and prey resource availability compared to other factors such as vegetation cover in determining recovery of vertebrate abundances is yet to be determined. Difficulties involved in simulating natural fires limit replication and, hence, data required for robust statistical analyses are lacking. Data presented here provide an indication of the amount of variation observed in diets of lizards that occur in habitats varying in vegetation recovery stages. In three of these four species, diet appears to be more conserved over the spatial scale of this study than it is over time.

Variation is the rule at all scales in the biological hierarchy. One must pick away at many potentially contingent factors to unmask the main structural components that drive ecosystem processes. We encourage more studies involving inter-specific ecological comparisons to consider variation in multiple dimensions by pulling apart diverse samples rather than lumping together all samples for a particular species. Here, basic natural history observations revealed a broad ecological concept of a dynamic realized niche meandering within the bounds of a more rigid fundamental niche space.

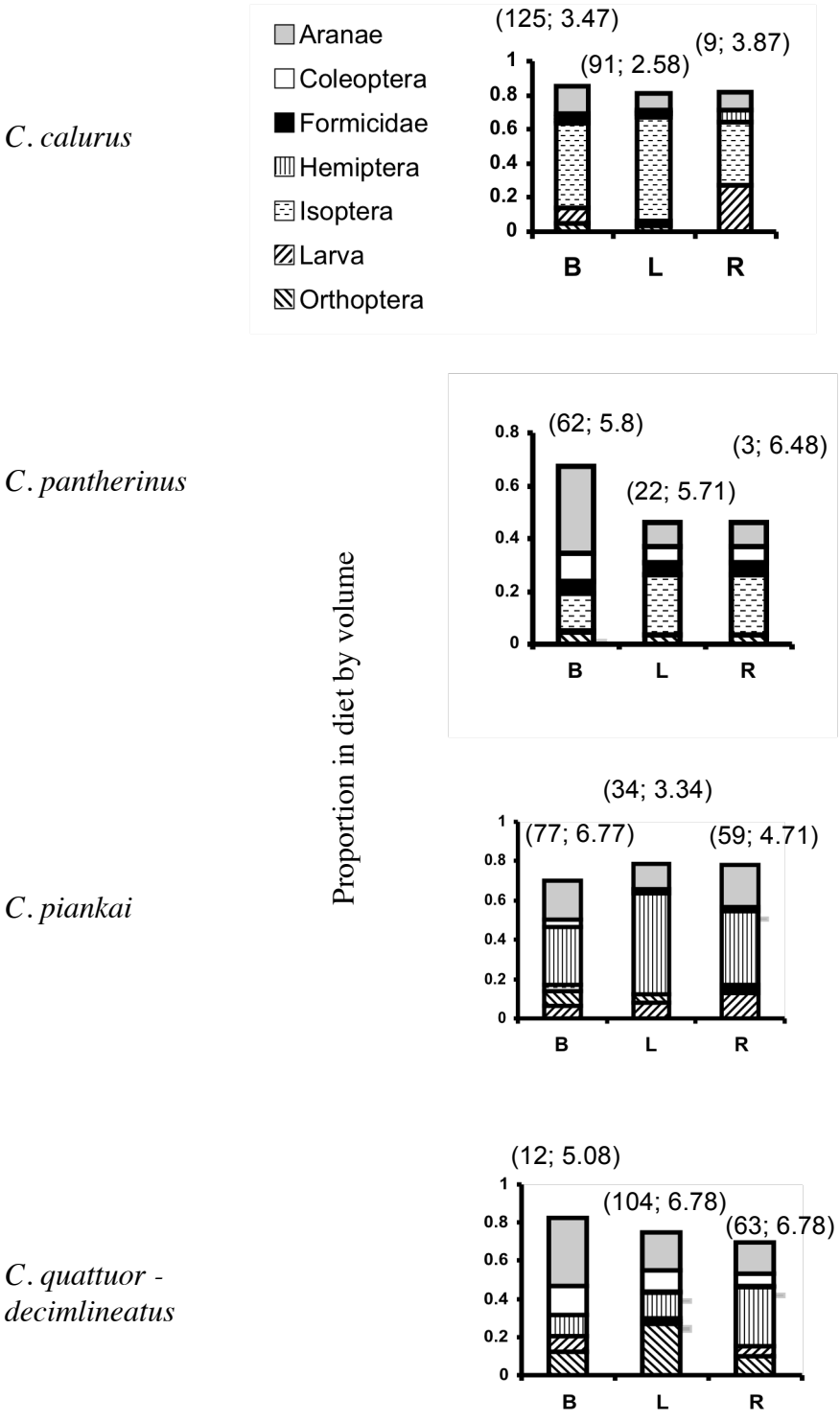

Figure 2: Dietary variation across space.

Dietary composition of the seven most commonly eaten insect types by four species of *Ctenotus* skinks comparing diet at three study sites in 1992. Sample sizes and dietary niche breadths based on Simpsons's diversity index (*D*) are given above each bar.

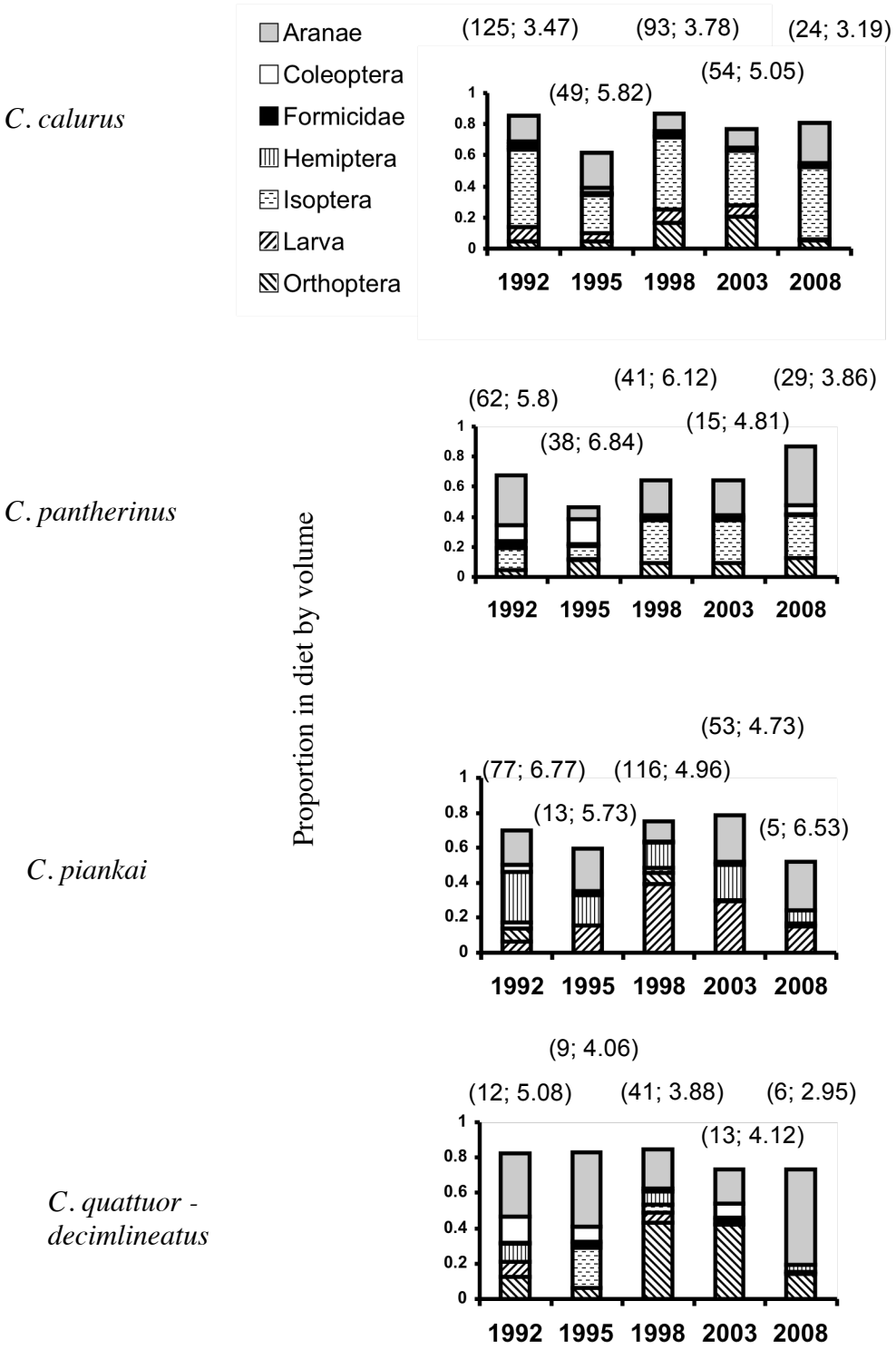

Figure 3: Dietary variation over time.

Dietary composition of the seven most commonly eaten insect types by four species of *Ctenotus* skinks comparing diet at the B-area study site during five censuses over a 16 year span. Sample sizes and dietary niche breadths based on Simpsons's diversity index (*D*) are given above each bar.

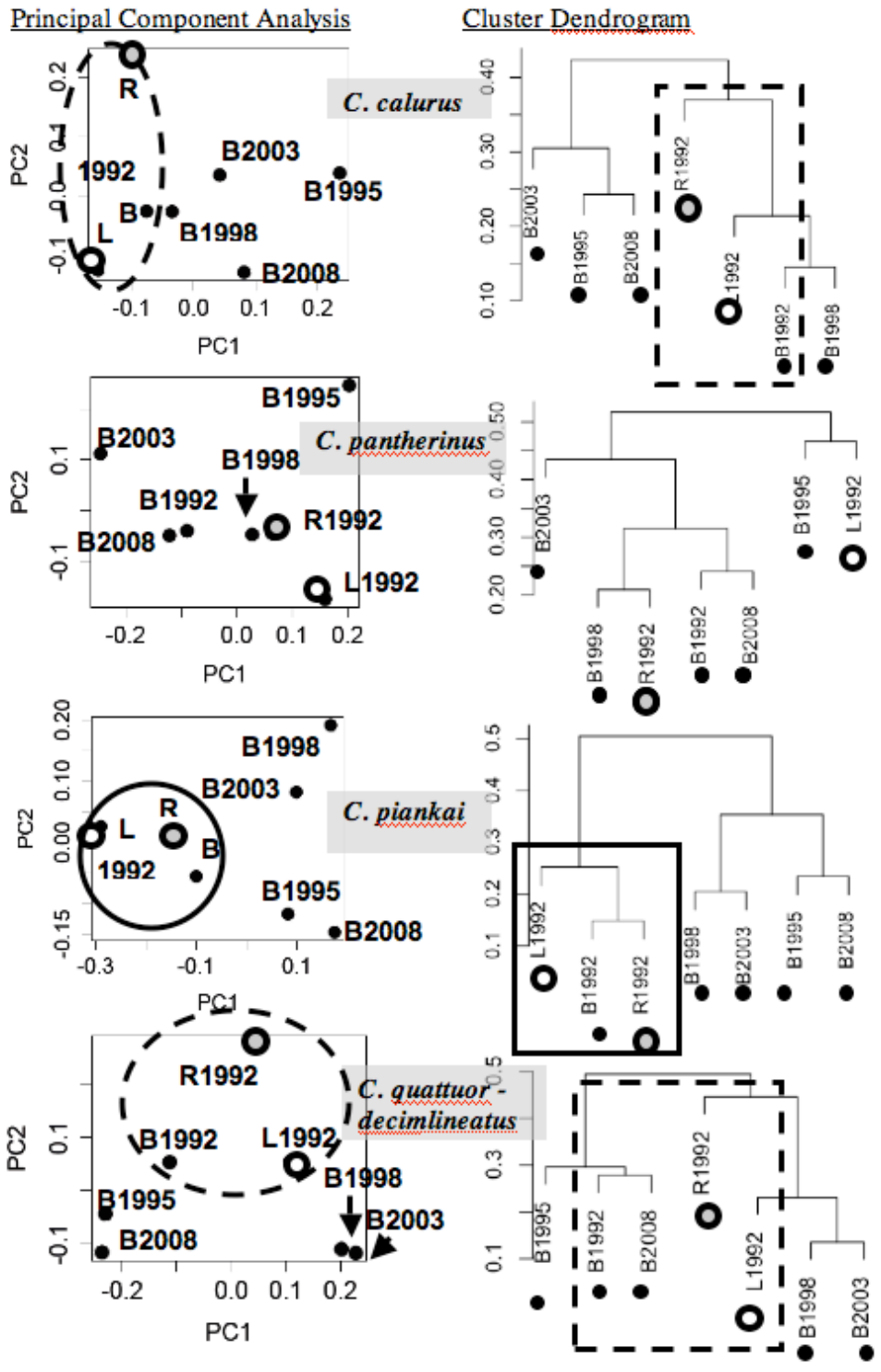

Figure 4: Individual species principal components plots of diet.

Principal components plots and associated cluster dendrograms showing graphically the similarities in diets for each species across spatial and temporal dimensions. Solid circles or squares indicate where samples from the same time (1992) cluster together. B area samples shown with small solid circles, those for the L and R sites with larger open circles. All 23 diet categories were used to make these plots.

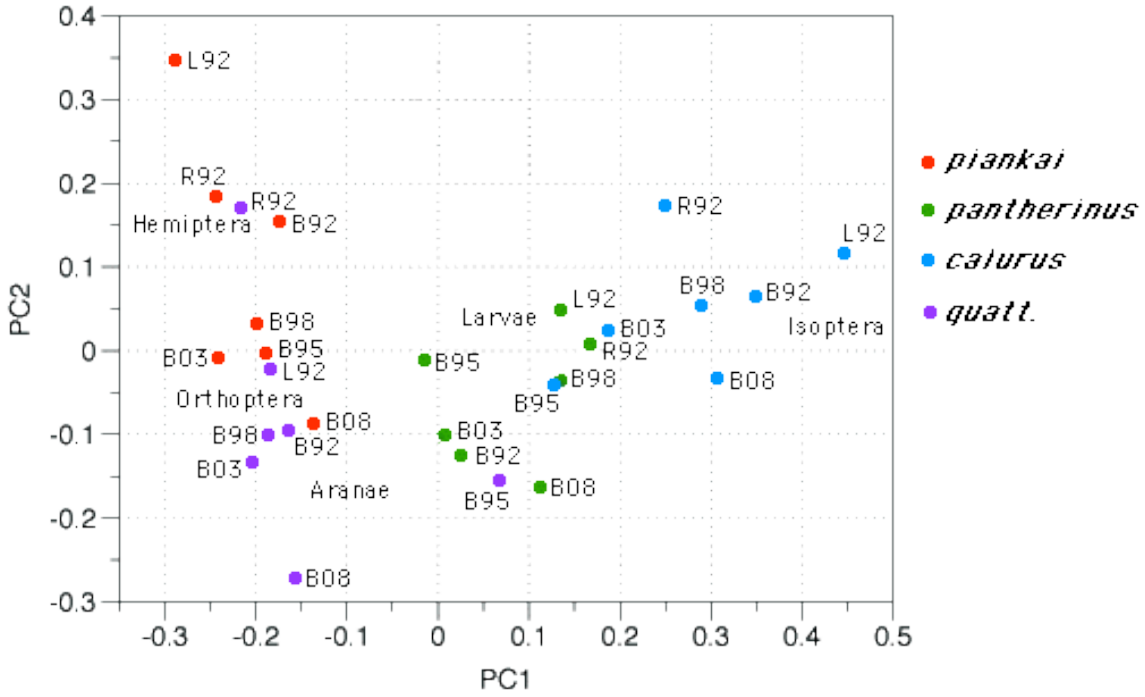

Figure 5: Combined species principal components plots of diet.

Principal components plot showing dietary niche space with all samples of four species combined. All 23 diet categories were used to make this plot. The first 2 components reduce variation by 60%. PC1 loads primarily on a Hemiptera-Isoptera axis and PC2 loads on Hemiptera-Orthoptera-Aranae axis. Because they eat Hemiptera, *C. piankai* are primarily in the upper left whereas termite eating *C. calurus* are on the right. *C. pantherinus* is intermediate. Samples for each species cluster together within relatively small areas of total niche space, an indication of dietary consistency and niche conservatism. Note some overlap between two pairs of species: *C. piankai* with *C. quattuordecimlineatus* and *C. calurus* with *C. pantherinus*.

Appendices

Appendix 1: CHAPTER 1 VOUCHER SPECIMEN LIST

All specimens examined for use in chapter 1 of this report have been deposited in the Western Australia Museum (WAM). Specimens with ERP catalogue numbers have not yet been catalogued by WAM. All snakes were collected by Eric R. Pianka. Only the most recently collected specimens have been catalogued by WAM. The following catalogue numbers are given separately for each species.

Brachyurophis semifasciatus: (WAM: R147038-R147068, R155069, R155071-R155074); (ERP: R1054, R1290, R2066, R2069, R2180, R3317, R23312, R23426, R23454, R23715, R23749, R23750, R25465, R25572, R25706, R25812, R27479, R27993, R31819, R32027, R32316, R32868, R32957).

Brachyurophis fasciolatus: (WAM: R147028-R147037, R155061-R155066); (ERP: R833, R26866, R26868, R26889, R28099, R28214).

Neelaps bimaculatus: (WAM: R147069-R147076, R155075-R155079); (ERP: R23353).

Simoselaps anomalus: (WAM: R147077-R147141, R156514-R156527); (ERP: R22943, R22944, R22949, R23105-R23110, R23139, R23140, R23382, R23424, R23425, R23524, R23525, R23682, R23683, R23751, R23765, R23766, R23784, R24006, R24317, R24627, R25726, R25742, R25807, R25813, R25836, R25844, R25850, R25852, R25987, R26018, R26262, R26763, R27009, R27011, R27238, R27247, R27248, R27356, R27381, R27484, R27489, R27538, R27615, R27619, R2767, R27675, R27676, R27947, R27957, R27982, R28004, R28010, R28070, R28071,

R28096, R28369, R32113, R32702, R33123, R33267, R33276, R33277, R33294, R33314, R33407, R33425, R33430, R33490, R33492, R33532, R33540, R33555, R33587, R34110, R34111).

Simoselaps bertholdi: (WAM: R147142-R147171, R155099-R155102, R156509-R156511), (ERP: R1236, R23110, R23374, R23453, R24493, R25729, R25846, R25987, R26108, R26157, R26243, R27226, R27266, R27267, R27364, R27366, R27389, R27394, R27443, R27485, R27491, R27537, R27946, R28293, R28594, R29166, R31231, R3246, R32610, R33775, R34004, R3645).

Appendix 2: CHAPTER 2 VOUCHER SPECIMEN LIST

All lizards for use in chapter 2 of this report were collected by Eric R. Pianka with the exception of lizards collected in 2008, which were collected by Eric R. Pianka and the author of this report. All specimens collected in 2003 and 2008 are deposited in the Western Australian Museum (WAM). Specimens with only ERP catalog numbers have not been catalogued by WAM but are currently in ERP's possession – negotiations are proceeding to arrange to deposit these in the Texas Natural History Museum in Austin, Texas. The following catalog numbers are given separately for each species.

Ctenotus calurus: (WAM: R155991-R155999, R156001-R156016, R156017-R156042, R156044-R156047, R169447-R169458, R169460-R169471); (ERP: B2041, B2088, B2119, B2197, B2201, B2211-B2212, B2245, B2250, B2284, B2306, B2313, B2314, B2371, B2376, B26521-B26523, B26525, B26528-B26529, B26531, B26534-B26535, B26538-B26539, B26557-B26559, B26562-B26564, B26568, B26570-B26572, B26575, B26586, B26596, B26601, B26621-B26622, B26626, B26633, B26645, B26658-B26659, B26663-B26664, B26667-B26674, B26696, B26698, B26708, B26717, B26739, B26743, B26780-B26787, B26794, B26804, B26808-B26809, B26816, B26820, B26833, B26845, B26847, B26850, B26855, B26899, B26901, B26903, B26922, B26924, B26928, B26979, B26981, B26989, B27020, B27022, B27026, B27215, B27221-B27222, B27276, B27279, B27283, B27286, B27312, B27316, B27349, B27353, B27354, B27451, B27452, B27499, B27502, B27505, B27507-B27508, B27560, B27602, B27604, B27624, B27628, B27633-B27634, B27894, B27903, B27905, B27917, B27926, B27930, B27959, B27960, B28021, B28059, B28101, B28194, B28220, B28222, B28225, B28270, B28298, B28323-B28325,

B28502-B28503, B28516, B28518, B28731, B28750-B28751, B28755, B28758-B28760, B28764, B28773, B28774, B28779, B28781, B28788-B28790, B28799, B28803, B28824-B28825, B28828, B28836-B28837, B28843, B28845, B28848, B28903, B28908, B28951, B28957-B29158, B29227, B29270, B29283, B30286, B30289, B30334, B30337-B30338, B30340-B30341, B30358, B30396, B30478, B30718, B30752, B30797, B30844, B30853, B30866, B31391, B31395, B31397, B31400, B31429, B31448, B31454, B31456, B31472-B31473, B31500, B31503, B31522-B31523, B31525, B31545, B31562, B31571-B31573, B31602-B31604, B31630, B31664-B31667, B31753, B31792, B31805, B31812, B31852, B31854, B31882, B31886, B31899, B31916, B31918, B31921-B31922, B31924-B31925, B31927, B31981, B32002, B32005, B32012, B32055, B32057, B32100, B32151, B32155, B32212, B32228, B32231, B32244, B32252, B32306, B32424, B32468, B32497, B32501, B32521, B32550, B32553, B32585, B32596-B32597, B32608, B32628, B32686, B32752, B32754, B32832, B32836, B32837, B32860, L26407, L26421, L26432-L26433, L26439, L26455, L26477, L26480, L26482, L27040, L27050-L27051, L27055-L27057, L27060, L27062, L27064, L27069, L27072, L27076, L27078, L27083, L27093, L27096-L27098, L27100, L27103-L27104, L27126, L27130, L27132, L27135, L27167, L27174, L27177, L27695-L27696, L27701, L27718, L27725, L27731, L27733, L27738-L27741, L27744-L27745, L27748-L27749, L27751, L27754-L27755, L27764, L27769, L27773, L27775, L27776, L27778, L27800, L27802, L27803, L27805, L27809, L27812, L27816, L27826, L27829, L27831, L27851, L27857, L27868, L27870, L27872-L27874, L27891, L28378-L28379, L28388, L28390-L28391, L28393, L28405, L28411-L28414, L28435, R26549, R26685, R26812, R26913, R27230, R27295, R27326, R27444, R28131).

Ctenotus pantherinus: (WAM: R155733-R155747, R169681-R169689, R169691-R169169694, R169696-R169699, R169701-169702, R169704-R169707, R169710-R159712, R169714-R169716); (ERP: B2079, B2167, B2375, B2383, B2385, B2401, B2404, B2407, B2429, B2487, B2491, B2495, B26530, B26536, B26540-B26541, B26543, B26545, B26561, B26565, B26569, B26573, B26582, B26589, B26599, B26617, B26624, B26629, B26632, B26648, B26656, B26660, B26715, B26771, B26772, B26774, B26796, B26803, B26830, B26856, B26906, B26918, B26930, B26974, B27014, B27016, B27218, B27308, B27310, B27453, B27494, B27500, B27509, B27582-B27583, B27625, B27679, B27902, B27914, B27928, B27962, B27963, B28016, B28102, B28104, B28172, B28191, B28193, B28200, B28224, B28294, B28327, B28373-B28374, B28479, B28489, B28497, B28501, B28505, B28515, B28529, B28532, B28554, B28567, B28570, B28730, B28747, B28754, B28765, B28771, B28780, B28793, B28801-B28802, B28805-B28806, B28809, B28820, B28822, B28827, B28831-B28832, B28844, B28846, B28854, B28904-B28906, B28910-B28912, B28915, B28918-B28919, B28950, B28953-B28954, B28956, B29023, B29038, B29130, B29264, B30872, B31402, B31420, B31478, B31482, B31506, B31524, B31673, B31686, B31700-B31701, B31735, B31810, B31897, B31929, B31963, B32128, B32166, B32172, B32276, B32299, B32305, B32744, B32814, B32838, B32844, B32862, B32900, B32997-B32998, L26409, L26427, L26435, L26445, L26448, L26461-L26463, L26479, L27042, L27049, L27122, L27181, L27699, L27790, L27825, L27827, L27846, L27876, L28440, L28447, L28466, R26703, R26800, R27400).

Ctenotus piankai: (WAM: R155769, R155771-R155786, R155788-R155802, R155805, R155807-R155821, R156078, R169425, R169427-R169430); (ERP: B2035-B2037, B2040, B2083, B2106, B2113, B2166, B2171, B2194, B2203, B2258, B2260,

B2285, B2303, B2309, B2315-B2317, B2332, B2333, B2374, B2405, B2424, B2449, B2478, B2488, B2490, B2493, B26566, B26607, B26699, B26701, B26795, B26814-B26815, B26819, B26844, B26849, B26854, B27015, B27017, B27025, B27029, B27199, B27202, B27206, B27300, B27302, B27304, B27336, B27337-B27339, B27372, B27432, B27434-B27435, B27464, B27523-B27525, B27559, B27561, B27575, B27592, B27611, B27652, B27656, B27892-B27893, B27895, B27897, B27906, B27908, B27921, B27923, B27937, B27964, B27970, B28019, B28022, B28053, B28064, B28065, B28066, B28106, B28156-B28157, B28159-B28160, B28162, B28192, B28201, B28241, B28242, B28257, B28269, B28271, B28279, B28283, B28307-B28308, B28326, B28358-B28359, B28362, B28742, B28744, B28777, B28804, B28817, B28857, B28914, B28952, B29184, B29265, B29311, B30292, B30750, B30757, B31407, B31425, B31427, B31455, B31479, B31496-B31497, B31561, B31661, B31668, B31692, B31738, B31754, B31790, B31811, B31813, B31855, B31858, B31982-B31983, B32007-B32008, B32048, B32050, B32061, B32091, B32092, B32095, B32149, B32153-B32154, B32157, B32159, B32162, B32209-B32211, B32230, B32232- B32233, B32268, B32290, B32292, B32304, B32323, B32326, B32330, B32337-B32341, B32381-B32383, B32428, B32498-B32499, B32520, B32527, B32570, B32572, B32576, B32617, B32620, B32624, B32682, B32685, B32723, B32725, B32749, B32781, B32791, B32810, B32816, B32830, B32833, B32834, B32835, B32858-B32859, B32866, B32906, B32920, B32947, B32979, B32986, L26406, L27079, L27081, L27084, L27088, L27117, L27123, L27150-L27151, L27192, L27700, L27713, L27717, L27767, L27768, L27782-L27783, L27813, L27836, L27838-L27839, L27842-L27843, L27863, L28380, L28382, L28400, L28403, L28406, L28421-L28423, L28439, L28465, R26678, R26693, R27007, R27257, R27288, R27294, R27373, R27378, R27423, R27457, R27510,

R27512, R27514, R27517, R27568, R27588, R27606, R27608, R27639, R27643, R27644-R27645, R27647, R27976-R27977, R27980, R27998, R28025, R28028, R28060, R28063, R28109, R28113, R28115, R28133-R28134, R28142, R28144, R28151-R28152, R28163, R28165-R28166, R28196-R28198, R28230-R28232, R28235, R28253, R28272, R28274, R28277, R28303, R28332, R28335, R28350, R28356).

Ctenotus quattuordecimlineatus: (WAM: R155978-R155990, R169813-R169816, R169861, R169867); (ERP: B2033, B2107, B2111, B2169, B2198, B2208, B2209, B2247, B2252, B2256, B2308, B2452, B26605, B26805, B26949, B27275, B27301, B27340, B27371, B27470, B27520, B27915, B28052, B28321, B28483, B28785, B28842, B29292, B30285, B30322, B30327, B30719, B30763, B30798, B31392, B31474, B31480, B31628, B31737, B31757, B32045-B32046, B32049, B32089-B32090, B32097, B32148, B32165, B32288, B32293, B32430, B32432, B32472, B32524, B32573, B32629, B32839, B32896-B32897, B32940, B32950, B32989, L26396-L26397, L26402, L26405, L26410, L26413-L26414, L26416-L26417, L26419, L26422, L26426, L26436, L26440, L26442-L26444, L26453, L26457, L26464-L26465, L26467, L26471-L26472, L26481, L26487-L26488, L26490, L26492, L27030-L27031, L27070, L27077, L27108, L27112, L27114, L27118, L27143-L27145, L27149, L27152, L27154, L27158-L27159, L27161, L27183-L27184, L27187, L27189, L27196, L27685, L27687, L27691, L27693, L27707-L27708, L27722-L27723, L27734, L27753, L27760, L27761, L27774, L27777, L27779, L27781, L27784-L27785, L27787, L27810-L27811, L27815, L27817-L27818, L27835, L27844-L27845, L27862, L27864, L27875, L27878-L27881, L27885, L28395-L28397, L28399, L28401-L28402, L28408, L28415-L28419, L28425, L28427, L28430, L28434, L28441, L28467, R26547, R26614, R26640-R26641, R26723, R26750, R26754-R26756, R26788-R26789, R26798, R26875-R26876, R26911, R26914-R26915, R26942, R26945, R26954, R26956-R26958, R26992, R27246,

R27250, R27293, R27296, R27343, R27345, R27374, R27420, R27428, R27436, R27456, R27458, R27461, R27511, R27515-R27516, R27566, R27649, R27670, R27978, R27988, R27990, R27999, R28037, R28094, R28110, R28114, R28116, R28184, R28229, R28254, R28256, R28263, R28273, R28275, R28305, R28306, R28315, R28318, R28344).

References

ARNOLD, S. J. 1972. Species densities of predators and their prey. American Naturalist 106:220-236.

BEAUPRE, S. J. 1995. Comparative ecology of the Mottled Rock Rattlesnake, *Crotalus lepidus*, in Big Bend National Park. Herpetologica 51:45-56.

BONANSEA, M. I., AND M. VAIRA. 2007. Geographic variation of the diet of *Melanophryniscus rubriventris* (Anura: Bufonidae) in Northwestern Argentina. Journal of Herpetology 41:231-236.

BOWEN, K. D. 2004. Geographic and size-related variation in the diet of insular populations of the Northern Watersnake. American Midland Naturalist 152:418-424.

BRAITHWAITE, R. W. 1987. Effects of fire regimes on lizards in the wet-dry tropics of Australia. Journal Tropical Ecology 3:265-275.

BROOKS, D. R., and D. A. MCLENNAN. 1991. Phylogeny, Ecology, and Behavior. University of Chicago Press, Chicago, Illinois.

CARPENTER, C. C. 1952. Comparative ecology of the common garter snake (*Thamnophis s. sirtalis*), the ribbon snake (*Thamnophis s. sauritus*), and butler's garter snake (*Thamnophis butleri*) in mixed populations. Ecological Monographs 22:235-258.

CHRISTIAN, K. A., C. R. TRACY, AND W. P. PORTER. 1984. Diet, digestion, and food preference of Galapagos Land Iguanas. Herpetologica 40:205-212.

DE QUEIROZ, A., HENKE, A., AND H. M. SMITH. 2001. Geographic variation and ontogenetic change in the diet of the Mexican Pacific Lowlands Garter Snake, *Thamnophis validus*. Copeia 2001:1034-1042.

ENGE, K. M. 2001. The pitfalls of pitfall traps. Journal of Herpetology 35:467-478.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1-15.

FERRATON, F., M. HARMELIN-VIVIEN, C. MELLON-DUVAL, AND A. SOUPLET. 2007. Spatio-temporal variation in diet may affect condition and abundance of juvenile European hake in the Gulf of Lions (NW Mediterranean). Marine Ecology Progress Series 337:197-208.

FILLIPI, E., L. RUGIERO, M. CAPULA, D. CAPIZZI, AND L. LUISELLI. 2005. Comparative food habits and body size of five populations of *Elaphe quatuorlineata*: the effects of habitat variation, and the consequences of intersexual body size dimorphism on diet divergence. Copeia 2005:517-525.

FITCH, H. S. 1975. Sympatry and interrelationships in Costa Rican anoles. Occasional Papers of the Museum of Natural History, The University of Kansas, Lawrence, Kansas. 40:1-60.

FOUQUETTE, M. J., JR. 1954. Food competition among four sympatric species of garter snakes, genus *Thamnophis*. Texas Journal of Science 6:172-189.

FYFE, G. 1980. The effects of fire on lizard communities in central Australia. Herpetofauna 12:1-9.

GARCIA, C. M., AND H. DRUMMOND. 1988. Seasonal and ontogenetic variation in the diet of the Mexican garter snake, *Thamnophis eques*, in Lake Tecocomulco, Hidalgo. Journal of Herpetology 22:129-134.

HAYDON, D. T., J. K. FRIAR, AND E. R. PIANKA. 2000. Fire Driven Dynamic Mosaics in the Great Victoria Desert I: Fire Geometry. Landscape Ecology 15:373-381.

HENDERSON, R. W. 1974. Resource partitioning among the snakes of the University of Kansas Natural History Reservation: A preliminary analysis. Milwaukee Public Museum Contributions in Biology and Geology 1:1-11.

HIBBITTS, T. J., E. R. PIANKA, R. B. HUEY, AND M. J. WHITING. 2005. Ecology of the Common Barking Gecko (*Ptenopus garrulus*) in southern Africa. Journal of Herpetology 39:509-515.

HOW, R. A., J. DELL, AND B. D. WELLINGTION. 1986. Comparative biology of eight species of *Diplodactylus* gecko in Western Australia. Herpetologica 42:471-482.

HOW, R. A., AND R. SHINE. 1999. Ecological traits and conservation biology of five fossorial "sand-swimming" snake species (Simoselaps: Elapidae) in southwestern Australia. Journal of Zoology (London) 249:269-282.

HUEY, R. B., E. R. PIANKA, AND T. W. SCHOENER. 1983. Introduction (pp. 1-6) In R. B. HUEY, E. R. PIANKA, and T. W. SCHOENER. (eds.), Lizard Ecology: Studies of a Model Organism. Harvard University Press, Cambridge, MA.

JAMES, C.D. 1991. Temporal variation in diets and trophic partitioning by coexisting lizards (*Ctenotus*: Scincidae) in central Australia. Oecologia 85:553-561.

JOSHUA, Q. I., M. D. HOFMEYR, AND B. T. HENEN. 2010. Seasonal and site variation in angulate tortoise diet and activity. Journal of Herpetology 44:124-134.

KEOGH, J. S. 1999. Evolutionary implications of hemipenial morphology in the terrestrial Australian elapid snakes. Zoological Journal of the Linnean Society 125:239-278.

KEOGH, J. S., R. SHINE, AND S. DONNELLAN. 1998. Phylogenetic relationships of terrestrial Australo-Papuan elapid snakes based on cytochrome b and 16S rRNA sequences. Molecular Phylogenetics and Evolution 10:67-81.

KEPHART, D. G., AND S. J. ARNOLD. 1982. Garter snake diets in a fluctuating environment: a seven-year study. Ecology 63:1232-1236.

KLAWINSKI, P. D., R. K. VAUGHAN, D. SAENZ, AND W. GODWIN. 1994. Comparison of dietary overlap between allopatric and sympatric geckos. Journal of Herpetology 28:225-230.

LEAVITT, D. J., AND L. A. FITZGERALD. 2009. Diet of nonnative *Hyla cinerea* in a Chihuahuan desert wetland. Journal of Herpetology 43:541-545.

LUISELLI, L. 2006. Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. Oikos 114:193-211.

LUISELLI, L., D. CAPIZZI, E. FILLIPI, C. ANIBALDI, L. RUGIERO, AND M. CAPULA. 2007. Comparative diets of three populations of an aquatic snake (Natrix tessellata, Colubridae) from Mediterranean Steams with different hydric regimes. Copeia 2007:426-435.

MAHAN, R. D., AND J. R. JOHNSON. 2007. Diet of the grey treefrog (*Hyla versicolor*) in relation to foraging site location. Journal of Herpetology 41:16-23.

MASTERS, P. 1996. The effects of fires-driven succession on reptiles in spinifex grasslands at Uluru National Park, Northern Territory. Wildlife Research 23:39-48.

MESQUITA, D. O., AND G. R. COLLI. 2003. Geographical variation in the ecology of populations of some Brazilian species of *Cnemidophorus* (Squamata, Teeidae). Copeia 2003:285-298.

PARKER, W. S., AND E. R. PIANKA. 1975. Comparative ecology of populations of the lizard *Uta stansburiana*. Copeia 1975:615-632.

PIANKA, E. R. 1969. Sympatry of desert lizards (*Ctenotus*) in Western Australia. Ecology 50:1012-1030.

PIANKA, E. R. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. Ecology 51:703-720.

PIANKA, E. R. 1971. Lizard species density in the Kalahari desert. Ecology 52:1024-1029.

PIANKA, E. R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4: 53-74.

PIANKA, E. R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences 71:2141-2145.

PIANKA, E. R. 1975. Niche relations of desert lizards. In M. L. CODY and J. M. DIAMOND (eds.) Ecology and Evolution of Communities, pp. 292-314. Harvard University Press, Cambridge, Massachusetts.

PIANKA, E. R. 1986. Ecology and Natural History of Desert Lizards. Analyses of the Ecological Niche and Community Structure. Princeton University Press, Princeton, New Jersey.

PIANKA, E. R. 1996. Long-term changes in lizard assemblages in the Great Victoria Desert: Dynamic habitat mosaics in response to wildfires. Chapter 8 (pp. 191-215) in M. L. CODY and J. A. SMALLWOOD (eds.) Long-term Studies of Vertebrate Communities. Academic Press, San Diego, California.

PIANKA, E. R. AND GOODYEAR. S. E. (in press). Lizard responses to wildfire in arid interior Australia: Long-term experimental data and commonalities with other studies. Austral Ecology.

REICHENBACH, N. G., AND G. H. DALRYMPLE. 1980. On the criteria and evidence for interspecific competition in snakes. Journal of Herpetology 14:409-411.

RODRÍGUEZ, A., M. NOGALES, B. RUMEU, AND B. RODRÍGUEZ. 2008. Temporal and spatial variation in the diet of the endemic lizard *Gallotia galloti* in an insular Mediterranean scrubland. Journal of Herpetology 42:213-222.

SCANLON, J., AND R. SHINE. 1988. Dentition and diet in snakes: adaptations to oophagy in the Australian elapid genus *Simoselaps*. Journal of Zoology (London) 216:519-528.

SCHOENER, T. W. 1977. Competition and the niche. In D.W. TINKLE and C. GANS (eds.), Biology of the Reptilia, Vol. 7, pp. 35-136. Academic Press, New York.

SENEY, E. E., AND J. A. Musick. 2007. Historical diet analysis of loggerhead sea turtles (*Caretta caretta*) in Virginia. Copeia 2007:478-489.

SHINE, R. 1977. Habitats, diets, and sympatry in snakes: a study from Australia. Canadian Journal of Zoology 55:1118-1128.

SHINE, R. 1984. Ecology of small fossorial Australian snakes of the genera *Neelaps* and *Simoselaps* (Serpentes, Elapidae). University of Kansas Museum of Natural History, Special Publication 10:173-183.

SIQUEIRA, C. C., M. VAN SLUYS, C. V. ARIANI, AND C. F. D. ROCHA. 2006. Feeding ecology of *Thoropa miliaris* (Anura, Cycloramphidae) in four areas of Atlantic Rain Forest, Southeastern Brazil. Journal of Herpetology 40:520-525.

STRAHAN, N. R., R. A. HOW AND J. DELL. 1998. Reproduction and diet in four species of burrowing snakes (*Simoselaps* spp.) from southwestern Western Australia. Records of the Western Australian Museum 19:57-63.

TOFT, C. A. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985:1-21.

TUTTLE, K. N., AND P. T. GREGORY. 2009. Food habits of the Plains Garter Snake (*Thamnophis radix*) at the northern limits of its range. Journal of Herpetology 43:65-73.

VALDERRAMA-VERNAZA, M., M. P. RAMÍREZ-PINILLA, V. H. SERRANO-CARDOZO. 2009. Diet of the Andean frog *Ranitomeya virolinensis* (Athesphatanura: Dendrobatidae). Journal of Herpetology 43:114-123.

VITT, L. J., AND G. R. COLLI. 1994. Geographical ecology of a Neotropical lizard: *Ameiva ameiva* (Teeidae) in Brazil. Canadian Journal of Zoology 72:1986-2008.

VITT, L. J., R. C. VAN LOBEN SELS, AND R. D. OHMART. 1981. Ecological relationships among arboreal desert lizards. Ecology 62:398-410.

VITT, L. J., P. A. ZANI, T. C. S. AVILA-PIRES, AND M. C. ESPÓSITO. 1998. Geographical ecology of the gymnophthalmid lizard *Neusticurus ecpleopus* in the Amazon rain forest. Canadian Journal of Zoology 76:1671-1680.

WEATHERHEAD, P. J., J. M. KNOX, D. S. HARVEY, D. WYNN, J. CHIUCCHI, AND H. L. GIBBS. 2009. Diet of *Sistrurus catenatus* in Ontario and Ohio: effects of body size and habitat. Journal of Herpetology 43:693-697.

WHELAN, R. J. 1995. The Ecology of Fire. Cambridge University Press, Cambridge, United Kingdom.

WHITE, M., AND J. A. KOLB. 1974. A preliminary study of *Thamnophis* near Sagehen Creek, California. Copeia 1974:126-136.

WINEMILLER, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs 60:331-367.

ZERBA, K. E., AND COLLINS, J. P. 1992. Spatial heterogeneity and individual variation in diet of an aquatic top predator. Ecology 73:268-279.

Vita

Stephen Edward Goodyear Jr. was born in Petersburg, Virginia and grew up in southern Virginia. Stephen developed an interest in reptiles at a young age and fostered that interest through books, visiting natural history museums and zoos, and keeping snakes and lizards as pets. Stephen began doing formal scientific research with snakes while an undergraduate at North Carolina State University.

Permanent address: 5906 Glenhollow Path, Austin, Texas 78745

This report was typed by Stephen Edward Goodyear Jr.